Epidemiology of seasonal falciparum malaria in an urban area of Senegal

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A 15-month longitudinal survey was carried out to examine entomological and parasitological aspects of human malaria transmission in Pikine, a city located in the Sudan savanna zone on the Cap Vert peninsula in the west of Senegal. The anopheline population was sampled twice weekly indoors by night human bait capture. During the same period, thick and thin blood films were collected from 296 children at 2-month intervals. Anopheles arabiensis was the only species responsible for transmission of Plasmodium falciparum. The parasite rate showed a positive correlation with both the entomological inoculation rate and the vectorial capacity. In Pikine, malaria is epidemic and probably unstable, and the population enjoys a variable degree of immunity.

Most studies of the dynamics of malaria transmission in Africa have been carried out in selected rural areas, where conditions could be well controlled because the groups involved were small, isolated, and easy to follow up.

The selection of a control strategy against malaria in the huge urban settlements which will characterize the world of the future requires the development of appropriate models that take into account social and environmental processes. Unfortunately, little work has been done in urban areas.

Our goals in the present study were to understand better the epidemiology of human malaria in the city of Pikine, Senegal, and to identify an effective method of reducing the effects of malaria through a primary health care programme.

BACKGROUND

Many studies have been carried out in rural areas of West and East Africa using epidemiological and mathematical methods. After the first mathematical model of Ross (33, 34), Macdonald (19-23) developed a model for the "force of infection". There then followed several reports of epidemiological observations (3, 8, 18), which provided in-depth knowledge of the bionomics of the local vectors and

transmission mechanisms. From measurements of epidemiological variables, in particular the vectorial capacity (12-14), it was possible to specify the risk of malaria and to predict the effects of possible interventions (10, 11, 25, 28, 29). Two exhaustive studies carried out in the Congo (5) and northern Nigeria (25) presented a synthesis of present knowledge on the transmission of malaria. However, neither model has been applied to urban areas.

No epidemiological studies have been carried out in Senegal, and only a few observations have been made in hospitals and health centres in Dakar, the capital city.

STUDY AREA

Climate

Cap Vert peninsula, located on the Atlantic coast of the Sudan savanna zone, has a mild wet climate, called "subcanarian". In Pikine, the mean relative humidity varies from 70% to 81%, except in December when it averages 56.8%, as a result of the predominance of northeasterly winds.

The hottest months are between June and October with a maximum temperature of 28.2 °C in October, and the coldest months are January-May with a minimum of 20.5 °C in March. In 1980, the total annual rainfall was 415 mm. The rainy season started at the end of July and lasted until mid-October.

Population

Pikine, 16 km from Dakar, is a new city which has experienced a demographic explosion as a result of a huge influx of people from rural areas after Senegal

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became independent in 1960 and of several mass relocation programmes for Dakar's slum population. In 1959, the population of the village of Pikine was estimated at 30 000. Today, there are about 450 000 inhabitants, mostly with low income and modest living standards.

In both the planned, urbanized area and several squatter settlements, the government provides piped drinking-water to public fountains. The dwellings are constructed of concrete and are occupied, on average, by 10 people. Few houses have electricity, and proper waste disposal facilities are unevenly distributed.

Surrounding the city there are many swamps, extensive market-gardens, and more than 2000 water-holes. A few of the local mosquito breeding-places are controlled by periodic applications of oil.

Transmission of malaria

Armengaud et al. (1), Ba & Maffre (2), Kane et al. (17), and Michel (24) have reported on the relative seriousness of malaria in Dakar and the incontestably seasonal transmission of *Plasmodium falciparum* by *Anopheles gambiae* s.l. According to Rey et al. (30), immunity is acquired quite slowly during the first 20 years of life because of the low level of endemicity and the shortness of the transmission period. The same group (31) also found that plasmodia carriers of rural origin came into Dakar and took some part in starting transmission, which culminates after the end of the rainy period, in October-November.

Seck (35) corroborated these data for the city of Pikine, and both he and Jancloes (16) showed that, in spite of the efforts exerted over many years, malaria was still a serious problem in the area. Statistical reports from the health centre in "old Pikine" indicated that, during the rainy season of 1979, 20.6% of outpatients presented with malaria.

MATERIALS AND METHODS

Throughout the present study, environmental conditions remained constant and attempts were made to avoid any changes in insecticide use or drug consumption.

Sample population

The survey was conducted in a geographically restricted section of the city rather than through a random sample of the 40 000 households in Pikine and the surrounding area. The section was selected on the basis of the willingness of its inhabitants to cooperate in the study, the presence of a very well accepted nurse, the availability of schoolrooms for medical examinations, the existence of an accurate

household census, and the feasibility of conducting home-visits twice weekly to capture mosquitos and to check the children's health status. Moreover, the mean distance between the homes in this section and the nearest health facility corresponded to the overall average for Pikine, i.e., about 0.8 km.

The area consists of blocks of buildings, with sandy dirt tracks laid out in quadrangles. It is located alongside a vast swamp, which dries up during the dry season. Some open wells are used to irrigate market gardens.

The inhabitants of the area reported using the following methods of malaria control: indoor spraying of insecticides (76%), mosquito-nets (30%), larvicides (19%), outdoor spraying of insecticides (8%), and chemoprophylaxis (6.3%).

The population in the section studied totalled 1481 (760 males and 721 females), of whom 52.5% were under 15 years of age and only 2.3% over 60 years.

Entomological study

Details of entomological procedures and results have been given elsewhere (36).

The anopheline population was sampled inside houses twice a week from October 1979 to December 1980. The man-biting capture method was carried out by 9 boys between 21h 00 and 06h 00. Several mosquito breeding sites were found in the area.

Mosquito collections were identified by species, age-graded, and examined for sporozoites. The sibling species of *Anopheles gambiae* s.l. were identified by Coluzzi, using nurse cell polytene chromosomes. The human blood index was determined on 150 mosquitos using the precipitation test.

Parasitological study

Between November 1979 and January 1981, thick and thin blood films were collected at 7 survey sessions at approximately two-month intervals (mean interval, 68 days), from a group of 296 children aged between 6 months and 6 years. Of this group, 59% were present at each of the 7 sessions, and 85% attended at least 5 of the sessions.

The blood films were stained with Giemsa. A 100 × oil-immersion lens was used to examine 100 fields of each thick film for trophozoites and gametocytes. In each of the gametocyte-positive thick films, the number of gametocytes per 1000 leukocytes was counted. Thin blood films were used to identify the *Plasmodium* species.

For each of the seven surveys, the following parasitological data were calculated: parasite rate (PR), trophozoite rate (TR), gametocyte rate (GR), and mean positive gametocyte density (MPGD). The theoretical mean gametocyte density (MGD) was calculated as the product of the MPGD and the GR. The

cumulative parasite rate was calculated for the 174 children who were present at each of the seven surveys.

RESULTS

Entomological study

A. arabiensis, a species of the dry savanna (6), is the only species responsible for malaria transmission in Pikine. The two other species found there, A. ziemanni (Grunberg, 1902) and A. pharoensis (Theobald, 1901) are of no importance in the transmission of malaria (36).

The monthly indices of the man-biting rate or vector aggressivity per child (m_1a) are shown in Table 1. The aggressivity per child was assumed to be one-third of the aggressivity per adult (4). Great seasonal changes in aggressivity were recorded, with an increase starting early in August, 8 days after the first rainfall, and a maximum in September $(m_1a = 34.8)$. Aggressivity then remained at a high level through December, decreasing afterwards to reach a minimum in March $(m_1a = 0.3)$. Six weeks before the first rainfall, aggressivity increased again. A significant positive correlation was found with temperature (r = 0.69, P < 0.01).

The average daily man-biting frequency (a) was derived from the frequency of biting (gonotrophic cycle) and the human blood index (HBI). The gonotrophic cycle was estimated to have a duration of at least 2 days during the high-transmission period; further studies are needed to confirm this. For Pikine, the HBI was 99%, a result that is probably an overestimate, since it was based exclusively on engorged females captured indoors (12). We assumed the true rate of anthropophily to be 90%, a high figure that is characteristic of urban areas. This gave a value of 0.45 for a.

The sporozoite index (s) also showed significant variation from month to month. The highest index was observed between October and December and the lowest between March and August (only one positive mosquito in 745 dissections). The average sporozoite index obtained from 5658 salivary glands was 0.0055 confidence limits, 0.0037-0.0080). This index is rather high because of the high rate of anthropophily.

Applying the basic formula of Davidson (7) adopted by Vercruysse & Jancloes (36), the mean daily survival rate of the vector (p) was estimated as 0.822 (see Annex 1).

The duration of the exogenous cycle (n) was obtained by applying the Moškovskij formula (9) which uses the average daily temperature as independent variable. Between January and May (cool period) the

duration was 20 days, compared with 11 days during the rest of the year (warm period).

Quantitative analysis. The entomological data collected permitted an analysis of the dynamics of malaria transmission, using the entomological inoculation rate (h_1) , the vectorial capacity (VC), and the index of stability (SI) (Annex 1). The results are summarized in Table 1.

The data indicate that malaria transmission takes place during the whole year at a very low level, but increases sharply at the end of the rainy season and the beginning of the dry season. More than 95% of the total annual transmission takes place at these times. In fact, most inoculations occur between September and February, with a daily inoculation rate per child of 0.076. This high level is associated with an average aggressivity of 12 bites per child per night and an overall sporozoite index of 0.0063. Between March and August, the probability of receiving one sporozoite inoculation a day is very low (P < 0.01).

Vectorial capacity from children to any other person also varied with time. Between June and December, high levels were found (VC = 2.41), while low values (VC = 0.4) were seen between January and May. The average over the year was 0.939.

The stability index was 2.3, showing that human malaria transmitted by A. arabiensis is unstable in Pikine.

Parasitological study

Blood film examinations indicated that *Plasmodium falciparum* (Welch 1897) is the predominant species. Only one child was found to be infected with *P. malariae* (Laveran 1891) on two different occasions. The origin of this parasite is unknown and its epidemiological significance in Pikine is negligible.

The bimonthly examination of blood films from children permitted seasonal fluctuations in the parasite, gametocyte, and trophozoite rates to be recorded (Table 2). The maximum parasite rate was 13.5% in January 1981, and the minimum 2.2% in August 1980, with an average value during the survey of 8.8%.

The trophozoite rate and the gametocyte rate decreased during the long dry season (January-August), increasing during the rainy season and at the beginning of the next dry season.

The fluctuations in the mean gametocyte density are also shown in Table 2. The minimum occurred in August (MGD = 0.009), the maximum in October (MGD = 2.0).

The cumulative parasite rate (Fig. 1) reflects the virtual absence of new episodes of patent parasitaemia in the period May-August. It is interesting that, of 41 positive children in November and

Table 1. Variations in entomological indices in Pikine, December 1979-December 1980^u

Month	Vector aggressivity (children) (m.a)	Sporozoite index (s)	Daily survival rate (p)	Length of exogenous cycle (days)	Probability of surviving n days (p")	Expectation of infective life (days) (EIL)	Vectorial capacity (VC)	Inoculation rate (h ₁)
December	8.4	0.0140	0.832	11	0.132	0.717	2.613	0.0900
January	5.3	0.0069	0.839	20	0.030	0.171	0.413	0.0366
February	3.5	0.0039	0.851	20	0.040	0.248	0.394	0.0136
March	0.3	0.0011	0.867	20	0.058	0.406	0.061	0.0003
April	9.0	0.0011	0.781	20	0.007	0.026	0.008	0.0007
Мау	6.0	0.0011	0.866	20	0.056	0.389	0.016	0.0010
June	1.2	0.0011	0.905	-	0.333	3.363	1.816	0.0013
July	2.6	0.0011	0.871	11	0.219	1.587	1.833	0.0029
August	9.8	0.0011	0.801	11	0.087	0.392	1.511	0.0095
September	34.8	0.0012	0.738	11	0.035	0.115	1.796	0.0418
October	13.4	0.0050	0.807	11	0.094	0.439	2.654	0.0670
November	10.0	0.0043	0.811	11	0.099	0.474	2.133	0.0430
December	8.4	0.0088	0.779	11	0.064	0.256	0.968	0.0739
Average	7.0	0.0055	0.822	14	0.064	0.326	0.939	0.0385

" See Annex 1 for explanation of the indices.

Month	No. examined	Parasite rate (%)	Trophozoite rate (%)	Gametocyte rate (%)	Mean positive gametocyte density (per 1000 leukocytes)	Mean gameto- cyte density (per 1000 leukocytes)
November	279	7.89	7.89	2.87	42	1.20
January	263	10.65	9.89	6.84	5	0.31
March	247	8.10	8.10	5.26	11	0.59
June	253	6.32	6.32	2.77	1	0.03
August	231	2.16	2.16	0.86	1	0.009
October	247	12.96	12.96	4.86	42	2.04
January	245	13.47	13.47	6.12	20	1.24
Average		8.79	8.65	4.25	18	0.78

Table 2. Variations in parasitological indices in children in Pikine, November 1979-January 1981"

See Annex 1 for explanation of the indices.

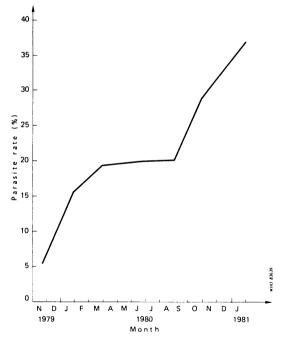


Fig. 1. Cumulative parasite rate observed among children in Pikine, November 1979-January 1981.

January, 30 had not had parasitaemia during the 5 previous surveys.

Quantitative analysis. Bekessy et al. (3) have developed a method that allows for the simultaneous approximation of recovery rate (\hat{r}) and incidence (\hat{h}) from longitudinal blood parasite surveys, assuming

that the rates do not vary between persons and during the survey intervals (see Annex 1). The results for Pikine, using this methodology, are summarized in Table 3.

The mean daily incidence was $\hat{h} = 0.00156$; on average, a new episode of patent parasitaemia started every 641 days. However, a 10-fold variation was observed during the survey.

The mean daily recovery rate was $\hat{r} = 0.015$; on average, parasites are eliminated from blood in $1/\hat{r}$ or 66 days. This recovery rate is 30% faster than Macdonald's estimate (21) for a non-immune population in West Africa ($\hat{r} = 0.0125$; $1/\hat{r} = 80$ days). The mean period required to eliminate parasites increased from 26 days in January to 132 days in June.

Equilibrium values of the average parasite rate, derived from the limit expression $\hat{h}/(\hat{h}+\hat{r})$ in the case of simple infection (3, 27), were reasonably close to the observed average parasite rate.

In the case of superinfections (19) the equilibrium value is given by the expression \hat{h}/\hat{r} , which is in this case 0.10, very close to the observed average parasite rate (0.088).

Relationship between entomological and parasitological data

Infectivity index. To examine the relationship between parasitological and entomological data, Macdonald (20) introduced a parameter, $b(=\hat{h}/h_1)$, to represent the proportion of the anopheline mosquitos with sporozoites in their glands that are actually infective. The observed infectivity index fluctuated each month, with an average of 0.0425. This means that about 4.25% of bites from infected mosquitos are able to produce patent parasitaemia (Table 4). Thus, on average, 24 infected bites are needed to

Table 3. Incidence of patent parasitaemia and recovery rate among children in Pikine, November 1979-January 1981"

Period	Interval between surveys (days)	°- Z	Ž	ষ	B	Incidence (<i>ħ</i>)	Recovery rate (f)	1/ĥ	1/?	$\hat{h}/(\hat{h}+\hat{r})$
November-January	56	23	13	0.0983	0.8125	0.00465	0.03849	215	26	0.108
January - March	70	80	14	0.0388	0.5600	0.000898	0.0122	1113	82	0.068
March-June	78	2	∞	0.0239	0.4444	0.000406	0.00754	2463	132	0.051
June-August	53	က	1	0.0143	0.8462	0.00061	0.0364	1639	27	0.016
August-October	98	25	4	0.1152	-	p	1	ı	1	Î
October-January	64	18	15	0.0861	0.5000	0.00202	0.0117	495	85	0.147
Average	89	82	65	0.0638	0.6132	0.00156	0.015	641	99	0.094

" See Annex 1 for explanation of the symbols.

 h N_I = no. of children negative at first survey and positive at second survey. ^ N₂ = no. of children positive at first survey and negative at second survey. ^ d $\alpha+\beta\geqslant 1$.

Table 4. Relationship between entomological and parasitological data collected in Pikine, January 1980–January 1981"

Month	ь	Inoculation rate (children) (h ₂)	Critical density (m ₁ *)	Critical man-biting rate (m ₁ *a)
January	0.1084	0.00458	4.5	2.0
March	0.4605	0.00284	0.70	0.3
June	0.0797	0.00216	0.30	0.13
August	0.1089	0.00330	3.18	1.4
January	0.0437	0.00233	5.16	2.3
Average	0.0425	0.00175	5.3	2.4

[&]quot; See Annex 1 for explanation of the symbols.

produce a single detectable infection in the peripheral blood. In March, the estimated proportion of bites resulting in an infection increased 4-fold (b = 0.46) to drop again in June (b = 0.08).

Parasitological inoculation rate (h_2) . Application of Macdonald's formula for h_2 yielded a value of 0.00175, using the average value of b of 0.0425 (Table 4). This indicates that a new infection is acquired every 571 days. The variation of h_2 was approximately half that of \hat{h} .

Relationship between sporozoite rate and gametocyte rate. Macdonald calculated the proportion of mosquitos that are infective from the proportion of people showing patent gametocytaemia. If x is the gametocyte rate in children and x_a the gametocyte rate in adults, the formula becomes (L. Molineaux, personal communication, 1982):

$$s = a (x + x_a) p^n / (a (x + x_a) - \log_e p).$$

Thus, x_a can be calculated from x and s, by rearranging the formula to give:

$$x_a = (s \log_e p - ax (s - p^n))/a (s - p^n).$$

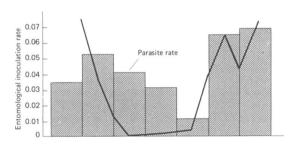
Using s = 0.0055 (Table 1) and x = 0.0425 (Table 2), we thus obtain a value for x_a of 0.08, i.e., the gametocyte rate is higher in those aged over 6 years than in those under 6 years of age. This is not surprising, as immunity develops very slowly in Pikine, and adults are bitten more frequently and are more numerous; they, rather than the young children, constitute the main reservoir of infection.

Critical level. Ross (32) outlined that the best way of analysing the possibility of the extinction of malaria transmission is via the "critical level of density". Macdonald (20) proposed a method of assessing this level (see Annex 1) and defined it as the

greatest density of mosquitos per capita within a community compatible with a progressive reduction in the prevalence of malaria to a negligible level. This method assumes that the probability of a mosquito surviving through one day is constant and known. The application of this method to the present study is summarized in Table 4.

Using the average yearly values calculated for Pikine, the critical density is $m_1^* = 5.3$ females, or $m_1^* = 2.4$. The average ma observed for children in Pikine was 6.4, almost 3 times the critical density. This implies that the biting mosquito population must be reduced by at least 63% of its present level to contain malaria transmission in Pikine.

Trends in parasite rate, entomological inoculation rate, and vectorial capacity. Fig. 2 compares the evolution of trends in the parasite rate (PR), the entomological inoculation rate (h_1) , and the vectorial capacity (VC). The parasite rate increased 6-fold between August and October, stayed at about the same level until January, and then decreased slowly to a minimum in August. The entomological inoculation rate (h_1) followed almost the same trend; it increased 11-fold between August and October, stayed fairly constant through December, and decreased from



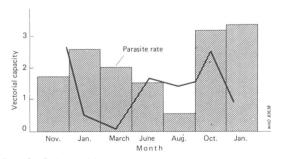


Fig. 2. Relationship between parasite rate, entomological inoculation rate and vectorial capacity in Pikine, November 1979–January 1981. In each graph, the columns represent the parasite rate; the single lines represent, respectively, the entomological inoculation rate and the vectorial capacity.

January to reach its minimum level in March. In June, there was an abrupt increase in vectorial capacity, which reached a maximum in October. The minimum occurred in March. These results give a clear indication that there are two distinct periods: a low-transmission period from February to June and a high-transmission period between September and December.

DISCUSSION

The present survey, dealing with entomological and parasitological aspects of human malaria transmission in Pikine, found only one important vector (A. arabiensis) and one parasite (P. falciparum). The parasite rate showed a positive correlation with both the entomological inoculation rate and the vectorial capacity. In particular, parasitological and entomological variables fluctuated in a similar fashion, with a simultaneous peak in September-October.

As for the urban factors that might influence the epidemiology of malaria in Pikine, it is worth mentioning that rural-urban migration patterns may be responsible for the importation of parasites. On the other hand, other factors associated with the urban environment, such as the high population density and easy access to antimalarial drugs, could be expected to reduce observed infection rates.

One problem is to determine how the vector acquires the gametocytes. Rey et al. (31) suggested that an importation of gametocyte carriers from rural areas might be responsible for the infection of urban A. arabiensis. However, the present study indicated that the inhabitants of Pikine are the main reservoir for vector infection. The increase in vectorial capacity observed in June is an essential determinant in the transmission cycle. At that time, the gametocyte rate in the resident population (2.77%) was sufficient for vector infection and increased transmission.

Recent studies in Ethiopia, Upper Volta, and elsewhere have indicated that A.arabiensis feeds predominantly on hosts other than man (37). This might explain the very low sporozoite index (s = 0.0031) recorded in Dori by Hamon et al. (15). In Pikine, A.arabiensis feeds almost exclusively on man owing to the scarcity of animals and the high density of the human population. This behaviour is consistent with the sporozoite index recorded during the study.

The observation in Pikine of a high vectorial capacity associated with a relatively low gametocyte

rate is not consistent with the results of other studies (25). This discrepancy could be the result of a low level of man-vector contact (through the use of repellents and mosquito-nets) or of a high consumption of antimalarial drugs.

The high consumption of chloroquine in Pikine seems to be related to the accessibility of health care centres. It is difficult to measure how much this access influences epidemiological parameters. Bekessy's methods do not adequately reflect the effects of superinfection and self-treatment.

As a result of fluctuations in endemicity, immunity among inhabitants of Pikine is likely to be variable. and is acquired very slowly. No statistical differences were observed between different age groups for PR, MPGD, \hat{h} , or \hat{r} . Furthermore, all age groups presented with the same acute clinical forms of P. falciparum malaria characterized by cerebral malaria. An average interval of 599 days between new infections might produce low immunogenic stimulation and might explain the discrepancies observed between parasitological data and clinical observations. Although the parasite index was lowest in August (2.2%), an outbreak of symptomatic malaria in children started in early July. The splenic index, which is usually an indicator of infection intensity, was found to be only 3.6%. This low splenic index may be due either to a low transmission level or to the consumption of antimalarial drugs.

Great differences are known to exist between different types of malaria, as various factors can affect the disease pattern. However, it is not easy to explain the unstable situation observed in the periurban environment of Pikine. Carnevale in Congo (5), Bekessy et al. in Nigeria (3), and Krafsur et al. in Ethiopia (18) performed longitudinal integrated malaria surveys. Their results indicated that stable endemic malaria can exist with seasonal fluctuations. The average incidence (\hat{h}) for children in Congo was 0.021, in Nigeria \hat{h} was 0.0145, and in Ethiopia \hat{h} was 0.0138; these rates imply that new infections are acquired every 47.5, 69, and 72 days. respectively. The average of these values yields a mean interval one-twelfth of the one observed in Pikine $(1/\hat{h} = 641 \text{ days})$, leading to the conclusion that in Pikine, malaria is epidemic and probably in an unstable situation, and that the population enjoys a variable degree of immunity. The great monthly differences observed in \hat{h} and \hat{r} are consistent with these conclusions. This instability suggests that it may be possible to control the malaria transmission cycle in Pikine.

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RÉSUMÉ

EPIDÉMIOLOGIE DU PALUDISME SAISONNIER À FALCIPARUM DANS UNE ZONE URBAINE DU SÉNÉGAL

Une enquête longitudinale de 15 mois sur les aspects entomologiques et parasitologiques de la transmission du paludisme humain a été faite à Pikine, qui est une ville de la zone de savane soudanaise sur la péninsule du Cap-Vert dans l'ouest du Sénégal. La population anophélienne a été échantillonnée deux fois par semaine à l'intérieur des habitations par des captures nocturnes sur appâts humains. En outre, des étalements en couche mince et en couche épaisse ont été recueillis à des intervalles de deux mois sur un groupe de 296 enfants de 6 mois à 6 ans pour y rechercher les parasites du paludisme.

Anopheles arabiensis s'est révélé être la seule espèce responsable de la transmission du paludisme. L'agressivité des ces anophèles accuse une variation saisonnière: elle aug-

mente à partir du début d'août, huit jours après les premières chutes de pluie, pour atteindre un maximum en septembre, le minimum étant en mars. L'indice parasitaire maximal a été observé en janvier (13,5%) et le minimal (2,2%) en août. L'indice parasitaire est en fonction directe à la fois du taux entomologique d'inoculation et de la capacité vectorielle.

Les auteurs en concluent que le paludisme est épidémique à Pikine et que la situation est probablement instable; la population jouit d'un degré variable d'immunité. Les fortes variations mensuelles de l'incidence de la parasitémie et du taux de guérison concordent avec ces conclusions. Le principal réservoir d'infection s'est révélé être la population adulte.

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Annex 1

SYMBOLS AND FORMULAE USED IN THE TEXT

anopheline density relative to the human population $(m_2, \text{ relative to adults}, m_1 \text{ to})$ children) average number of persons bitten by one a:*p*:

mosquito in a day (a was assumed to be 0.45)

man biting rate (vector aggressivity) in m_1a : children

man biting rate (vector aggressivity) in m_2a :

observed sporozoite rate So:

m:

time taken for completion of exogenous n: cvcle

mosquito daily survival rate =

number of parous female mosquitos total number of female mosquitos

 p^n : a mosquito's probability of surviving through *n* days

h_1 :	entomological inoculation rate in children; $h_1 = m_1 as$		α = proportion of positive subjects at the second survey among those negative at the first;
SI:	stability index; represents the number of bites on man taken by the average mos- quito during its lifetime;		β = proportion of negative subjects at the second survey among those positive at the first.
EII.	$SI = a/(-\log_e p)$	$\hat{h}/(\hat{h}+\hat{r})$	expected equilibrium parasite rate
EIL:	mosquito's expectation of infective life; $EIL = p''/(-\log_e p)$	1/ ĥ :	expected duration of a new infection
VC:	vectorial capacity from children to anybody;	$1/\hat{r}$:	expected duration of an episode of parasitaemia
PR: TR:	$VC = m_1 a^2 p^n / (-\log_e p)$ parasite rate trophozoite rate	<i>b</i> :	the proportion of the anophelines with sporozoites in their glands that are actually infective;
GR:	gametocyte rate $(=x_0)$		$b = \hat{h}/h_1$
MPGD: MGD:	mean positive gametocyte density mean gametocyte density (MGD = MPGD × GR)	s_{c} :	calculated sporozoite rate; $s_c = ax p^n / (ax - \log_e p)$
ĥ:	incidence; $\hat{h} = (\alpha/t) (\alpha + \beta) \log_e 1/(1 - (\alpha + \beta))$	<i>X</i> _a :	expected gametocyte rate in adults; $x_a = (s \log_e p - ax (s - p^n))/a(s - p^n)$
r̂:	recovery rate; $\hat{r} = (\beta/t) (\alpha + \beta) \log_e 1/(1 - (\alpha + \beta))$	<i>h</i> ₂ :	parasitological inoculation rate (children); $h_2 = m_1 a^2 bx p^n / (ax - \log_e p)$
	where $t = \text{time interval between surveys};$	m_1^* :	critical level of density; $m_1^* = \hat{r} \log_e p/a^2 bp^n$